ARTHROPOD POPULATIONS IN A HEATHLAND AS RELATED TO CYCLICAL CHANGES IN THE VEGETATION

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Investigations of the changes in the vegetation and micro-climate of a *Calluna* dominated heath have been made at Elsick House in Kincardinshire near Cammachmore, Scotland (Grid. Ref. No. 887952). The site and the vegetation are described in Barclay-Estrup & Gimingham (1969). The study was concerned with the changes that take place in a vegetation patch during the life cycle of the dominating plant *Calluna vulgaris* (L.) Hull. The changes in *Calluna* affect not only the vegetation of the patch, but also the microclimate. The microclimate of the patches is described in Barclay-Estrup (1971).

The life cycle of heather has been arbitrarily divided by Watt (1947) into four phases: pioneer, building, mature and degenerate. The changes in the vegetation and the microclimate can be briefly described as follows from Barclay-Estrup (1971):

Pioneer Phase

C. vulgaris individuals up to 3–10 years of age; contributing about 10% of total 'overstorey' cover. Remaining cover from bryophytes (abundant) and other vascular plants, here at their maximum (70% 'overstorey' cover). Biomass of *Calluna* low, but net production in young shoots, although low per unit area, is high in relation to biomass. Microclimate characterized by extremes: illumination at ground level high; temperatures high on days of strong insolation, night and winter temperatures often low; saturation deficits sometimes high; air-movement at a maximum; through-fall of precipitation maximal. In the pioneer phase the community dominant has minimal influence upon the rest of the vegetation.

Building Phase

C. vulgaris individuals 7–13 years of age; contributing about 85% of total 'overstorey' cover. Representation of associated species minimal. Biomass of *Calluna* ranks second only to that in mature phase; net production in young shoots at maximum. Microclimate profoundly affected by the closed, dense canopy of *Calluna*: illumination at ground level reduced to as little as 2% of outside light; temperatures generally lower than at other stages, but higher during the night and briefly during winter; saturation deficit always low; air-movement negligible; interception of precipitation at a maximum. In the building phase *Calluna* exerts its greatest effects upon the environment and excludes most other species.

Mature Phase

C. vulgaris individuals 12–28 years of age; contributing about 75% of 'overstorey' cover. Increasing cover of other species, particularly bryophytes. Biomass of *Calluna* at its maximum, net production of young shoots slightly less than in building phase. Microclimate still strongly influenced by *Calluna* canopy, but shows some changes: illumination at surface increases to about 20% of that in the open; higher and lower temperatures than in building phase, but extremes not yet great; saturation deficit still low; air-movement still greatly restricted; interception of rainfall still considerable. In the mature phase, the vigour of the dominant *Calluna* is declining and its effects on the microclimate are consequently lessened. Conditions become somewhat more favourable for other species, which begin to re-invade the area.

Degenerate Phase

C. vulgaris individuals 16–29 or more years of age; contributing now only 35% of 'overstorey' cover. Other species much more prominent, with bryophytes at their maximum. Biomass of *Calluna* still relatively high compared to the pioneer phase: but net production in young shoots/unit area now at a minimum. Microclimatic factors approach—sometimes exceed—the extremes of the pioneer phase: illumination at the centre of the gap up to 57% of that in the open, temperature amplitude at surface approaching that of pioneer phase, soil temperatures often higher, atmosphere close to the ground subject to increased saturation deficits on warm days, air-movement greater, interception of rainfall reduced to a level approaching that of pioneer phase. In the degenerate phase a gap develops in the centre of the *Calluna* bush and gradually increases in diameter. The decreasing dominance of *Calluna* results in conditions more suitable to a variety of associated species, and also to the establishment of *Calluna* seedlings which may then initiate a new cycle.

The phases of *Calluna* in a mature heath such as at Elsick House are randomly dispersed and present a mosaic of habitats to arthropods and other animals. Even though the distances are small (0.5 to 1.5 m) vegetational and microclimatological differences may be large—thereby affecting animal populations. Cherrett (1964) noted with reference to a population of spiders that 'this diversification of the ecological requirements of the species present results in apparently small variations in the physical factors of the habitat being associated with significant changes in the species present and in their density'. Vlijm & Kessler-Geschiere (1967) have shown the response of some wolf spiders to small variations in habitat.

METHODS

Four sites were sampled, one for each phase of *Calluna*. These sites were in an area where *Vaccinium vitis-idaea* L. is a sub-dominant to *Calluna*. The sampling system used was designed to measure seed dispersal, but also acted as an effective pitfall trapping system. In each of the four test sites five 5 × 2.5 cm glass specimen tubes were placed at 25 cm intervals in a line along a diameter of the individual *Calluna* plant of a particular phase. The tubes were inserted into litter or moss layer till the tops were about 1 cm from the surface. In the course of the experiment the tops of the vials were usually very close to the surface, as fresh litter was deposited and there was growth by the mosses.

The tubes were left in position for two week periods (except on one occasion for a three week period due to a heavy snowfall). Initially, between 14 September, 1964 and 22 February, 1965 records were limited to the total numbers of arthropod individuals caught. From 22 February to 1 November, 1965, all spiders, phalangids and ants were preserved in 70% alcohol; specimens belonging to other groups were counted and discarded. All the spiders and the ants have been identified to species. In the other groups the identification has been to class level.

TABLE 1.—ARTHROPOD CAPTURES IN RELATION TO THE HEATHER PHASE

Phase	*Ants*	*Arachnids*	*Centipedes*	*Millipedes*	*Misc. Arthr.*	*Total Arthr.*	*Spiders*	*Phalangids*
Pioneer	352	208	15	3	221	799	84	84
Building	87	132	43	11	123	396	29	63
Mature	96	198	70	9	258	631	41	97
Degenerate	353	282	28	1	217	881	67	118

TABLE 2—NUMBERS TRAPPED PER PHASE FOR THE FAMILY LYCOSIDAE

	Pioneer	*Building*	*Mature*	*Degenerate*
Lycosa pullata ...	13	0	0	9
L. nigriceps ...	6	7	7	4
Tarentula pulverulenta	17	0	8	13
Trochosa terricola ...	8	1	2	2
Totals ...	44	8	17	28

RESULTS

Arthropod activity was noted at Elsick heath at all times of the year. Flights of Diptera were observed on days with the air temperature as low as 3° C and with snow cover on the ground. Flying insects were observed; however, only ground arthropods were captured and the totals for the period 14 September, 1964 to 1 November, 1965, are shown in Table 1.

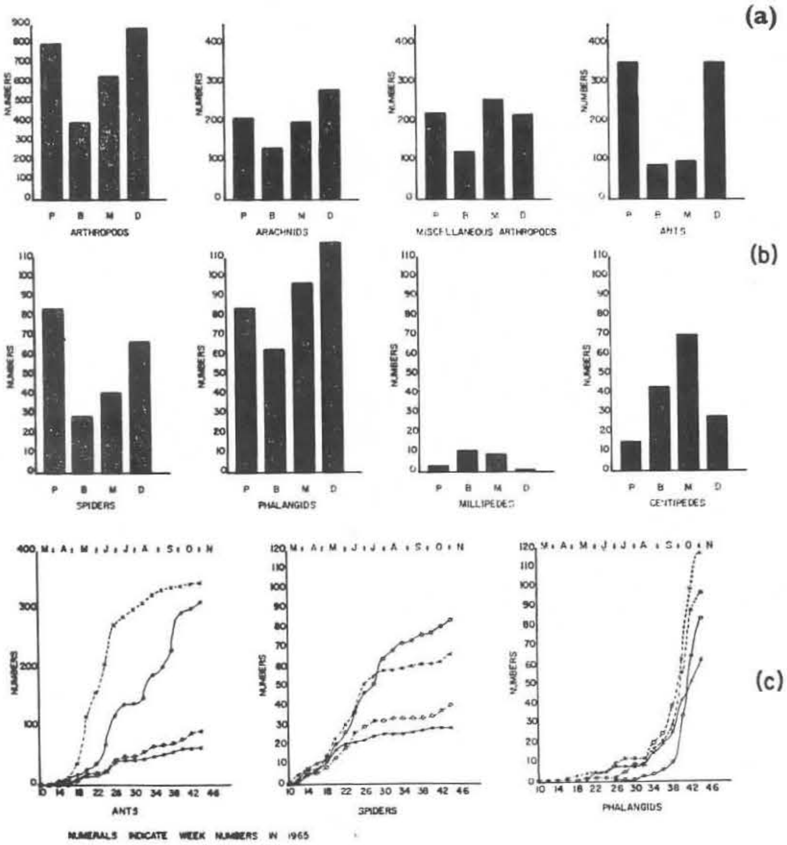

Fig. 1.—Arthropod populations (a) Total of all arthropods collected in *Calluna* phases; (b) histograms of total numbers of various groups collected in each phase area; (c) cumulative frequency distributions of indicated groups in each phase in 1965 (months indicated at tops of graphs).
-o-, P, Pioneer; -x-, B, Building; —o—, M, mature; —x—, D. Degenerate.

Total arthropod population frequencies are shown in fig. 1–(a). Each point represents a four week period (except one five week period, 18 January to 22 February, 1965). The histograms in fig. 1–(b) depict populations in relation to *Calluna* phases. The trends are similar in all groups, with the pioneer and degenerate phases having the greatest numbers.

Exceptions are: (1) miscellaneous Arthropoda (mainly Collembola) where larger numbers are found in the mature phase; (2) phalangids where habitat preference is for the mature and degenerate phases; and (3) millipedes, the only group which indicates the building phase as the preferred habitat.

Fig. 1–(c) shows some trends in the populations concerned. These graphs are of populations for the period 22 February to 1 November, 1965.

All ant and spider specimens have been checked and identified to species. All other groups were not checked. The ants are represented at Elsick by a single species, *Myrmica ruginodis* Nylander. Thirty-two species of spiders in seven families have been identified. A total of 58 females and 121 males were identified. Tabulation shows that the number trapped per phase was pioneer 66, building 25, mature 39 and degenerate 49. The number of species per phase, in the same order, is 17, 13, 15 and 17. Of the identified specimens only the Lycosidae had sufficient numbers to be indicative of phase preference as shown in Table 2.

SPECIES LIST

Only identified specimens are included in this list with nomenclature according to Locket & Millidge (1951–53). All identifications are by J. M. Cherrett. Numbers of individuals for each species are in brackets following each name.

CLUBIONIDAE: *Agroeca proxima* (O.P.-Cambridge), (2 ♀, 2 ♂).

THOMISIDAE: *Oxyptila trux* (Blackwall), (2 ♂).

LYCOSIDAE: *Lycosa pullata* (Clerck), (9 ♀, 13 ♂), *L. nigriceps* (Thorell), (4 ♀, 20 ♂), *Tarentula pulverulenta* (Clerck), (10 ♀, 28 ♂), *Trochosa terricola* (Thorell), (6 ♀, 7 ♂).

AGELENIDAE: *Hanhia montana* (Blackwall), (1 ♀).

MIMETIDAE: *Ero cambridgei* (Kulczynski), (1 ♀).

TETRAGNATHIDAE: *Pachygnatha degeeri* (Sundevall), (4 ♀, 1 ♂).

LINYPHIIDAE: *Ceratinella brevipes* (Westring), (1♀, 5 ♂). *Walckenaera acuminata* (Blackwall), (2 ♀, 1 ♂), *Wideria antica* (Wider), (1 ♀, 5 ♂), *Trachynella nudipalpis* (Westring), (6 ♂), *Dicymbium nigrum* (Blackwall), (1 ♂), *Metopobactrus prominulus* (O.P.-Cambridge), (1 ♀, 1 ♂), *Gonatium rubens* (Blackwall), (7 ♀), *Maso sundevalli* (Westring), (1 ♀, 2 ♂), *Peponocranium ludicrum* (O.P.-Cambridge), (2 ♀, 3 ♂), *Pocadicnemis pumila* (Blackwall), (1 ♂), *Minyriolus pusillus* (Wider), (1 ♂), *Tapionocyba pallens* (O.P.-Cambridge), (1 ♂), *Monocephalus fuscipes* (Blackwall), (2 ♂), *Micrargus herbigradus* (Blackwall), (1 ♂), *Macrargus rufus* (Wider), (2 ♂), *Centromerus sylvaticus* (Blackwall), (3 ♀, 5 ♂), *C. arcanus* (O.P.-Cambridge), (1 ♀, ♂), *C. dilutus* (O.P.-Cambridge), (1 ♂), *Oreonetides abnormis* (Blackwall), (1 ♀), *Bolyphantes luteolus* (Blackwall), (1 ♀), *Lepthyphantes zimmermanni* (Bertkau), (6 ♂), *L. ericaeus* (Blackwall), (2 ♂), *Mengea scopigera* (Grube), (1 ♂).

DISCUSSION

The total arthropod population shows significant differences between the phases of *Calluna*, indicating quite different microenvironments. It is also obvious that population peaks are reached at different times in the various phases. The large decrease in total population that occurred in late July and early August should perhaps be regarded as somewhat abnormal as the July mean temperature was 2.7° C. below average and the lowest recorded since 1856 (Monthly Weather Report, July 1965). It is interesting that in spite of the relatively low temperature there was only a very small decrease in the population of the building phase area and even a small population increase in the mature phase area. Overall, the degenerate phase seems to be the most favourable phase for arthropod activity.

Interpretation of the ant population is simplified as there is only one species present. *Myrmica ruginodis* is the commonest British ant and has a wide ecological amplitude (Wragge Morley, 1953). However, while these ants are able to utilize many habitats, they are not found in areas that are relatively infertile (low food supply) or that are cool in early summer (Brian, 1964). Colonies studied in west Scotland show a direct correlation with degrees of insolation. Colonies are larger and individuals are larger in areas with higher insolation. Higher insolation produces a more favourable temperature condition and a richer food supply (Brian & Brian, 1951). On this basis it would be expected that the pioneer phase should have a consistently high population, but this was not the case in the sample site during 1965. Another factor is probably important here. It was noted that heavy rainfalls did a great deal of damage to ant nests in the pioneer phase. Brian (1956) states that the ideal site is '. . . hot, windless, humid, mechanically resistant, rain impervious for nesting. . .'. This description more nearly fits the degenerate phase with temperatures near to those of the pioneer phase, but still some protection from wind and rain by the aging *Calluna* bush. The graphs of the populations at Elsick show a significant preference by *Myrmica ruginodis* for the pioneer and degenerate phases with the degenerate indicated as the better of the two.

The arachnids, when taken in total, do not show as large differences between the phases as did the ants. When the arachnids are separated into spiders and phalangids greater differences are noticed. The spiders prefer the pioneer and degenerate phases. Food supply is probably the important factor in this predaceous group. The phalangids show a very different pattern of distribution from the spiders and ants, both in relation to phase and peak population periods. This group prefers a damp shaded habitat (Ross, 1948) and is not present in large numbers until late summer when all the phases provide such a habitat. As would be expected, there are not such large differences here as in the spider and ant populations. The fact that a large population increase begins last in in the warmest and driest phase, the pioneer, would seem to confirm that the phalangids prefer a cool and moist habitat and occupy an area when such conditions are established.

The millipedes and centipedes are interesting in that both groups seem to prefer the building and mature phases. In fact, the millipedes are the only group to show a preference for the building phase. The centipedes have a late summer maximum population, but still inhabit the cooler building and mature phases in preference to the degenerate and pioneer. This is noteworthy in view of the tendency for centipedes to be nocturnal (Ross, 1948); during the night the building and mature phases are warmer than the other two phases.

The results of this present study indicate that for heathlands dominated by *Calluna* the phase of individual *Calluna* plants should be considered when investigating population distributions.

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SUMMARY

During its life cycle *Calluna vulgaris* (L.) Hull passes through four phases: pioneer, building, mature, and degenerate. In each phase *Calluna* varies as to cover, biomass, and net productivity; the phase of *Calluna* affects the associated plant species, microclimate, and arthropod populations. In the pioneer phase, when the microclimate is most extreme, arthropods are numerous and spiders are at a maximum, but numbers for total Arthropoda are not as high as in the degenerate phase. In the building phase *Calluna* is very vigorous and greatly modifies the microclimate. Arthropods are at a minimum in this phase. In the mature phase *Calluna* is beginning to decline and other plant species are increasing. The arthropod population is increasing in this phase as compared with the building phase. The last phase, the degenerate phase, has the greatest arthropod populations. The degenerate phase is a phase of extremes in microclimate similar to the pioneer phase, but the declining *Calluna* plant provides more cover than does the pioneer phase plant.

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[Dr. Barclay-Estrup's results do not appear to us to support the interpretation he places on them. The catches of Arthropoda in pitfall traps depend on both their abundance and *their activity*. Arthropods can be expected to be more active in the less obstructed, more open pioneer and degenerate phases of *Calluna* growth and more of them will fall into pitfall traps. A more detailed paper on this subject is in preparation.—Eds.]